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FORAGING BEHAVIOR OF TAWNY EMPEROR CATERPILLARS (NYMPHALIDAE: *ASTEROCAMPA CLYTON*)

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ABSTRACT. Tawny emperor caterpillars moved up to 3 m to new feeding sites, passing by numerous leaves in the process. These cryptic larvae molted on the underside of leaves or between leaves they tied together before feeding at the new sites.

Cryptic and thus presumably palatable caterpillars may avoid their natural enemies by feeding on the underside of leaves, foraging at night, commuting to and from feeding sites, moving some distance between feeding bouts and cutting off leaf remains after feeding on leaves (Heinrich, 1979). This appears to be a consequence of birds learning to forage preferentially on plants with caterpillar-damaged leaves (Greenberg & Gradwohl, 1980; Heinrich & Collins, 1983). Parasitoids also use damaged leaves and frass to locate caterpillars (Sato, 1979).

Tawny emperor caterpillars (*Asterocampa clyton flora* (Edwards): Nymphalidae) are of particular interest here, because they aggregate in the early instars, in contrast to most cryptically-colored caterpillars. By aggregating, these caterpillars may cause considerable leaf damage at a feeding site and thus, draw attention to themselves in a way that early instars of solitary, cryptic larvae would not. The objective of this study was to examine the foraging behavior of early instar tawny emperor caterpillars.

METHODS

The caterpillars were observed on hackberry trees (*Celtis laevigata* Willdenow) at the University of Florida (Gainesville) in fall 1981. Egg clusters were located on the underside of leaves on the distal portion of major branches. Larval aggregations were followed by placing labeled bands on leaf petioles of occupied leaves. Each day caterpillars were censused by searching leaves of the main branch with the egg cluster. During the molting periods these censuses provided a reliable record of total surviving larvae. However, during feeding bouts caterpillars were often moving back and forth along the branches and thus difficult to census accurately. Consequently, only larvae on leaves were censused. Leaf tissue eaten by the caterpillars was estimated to

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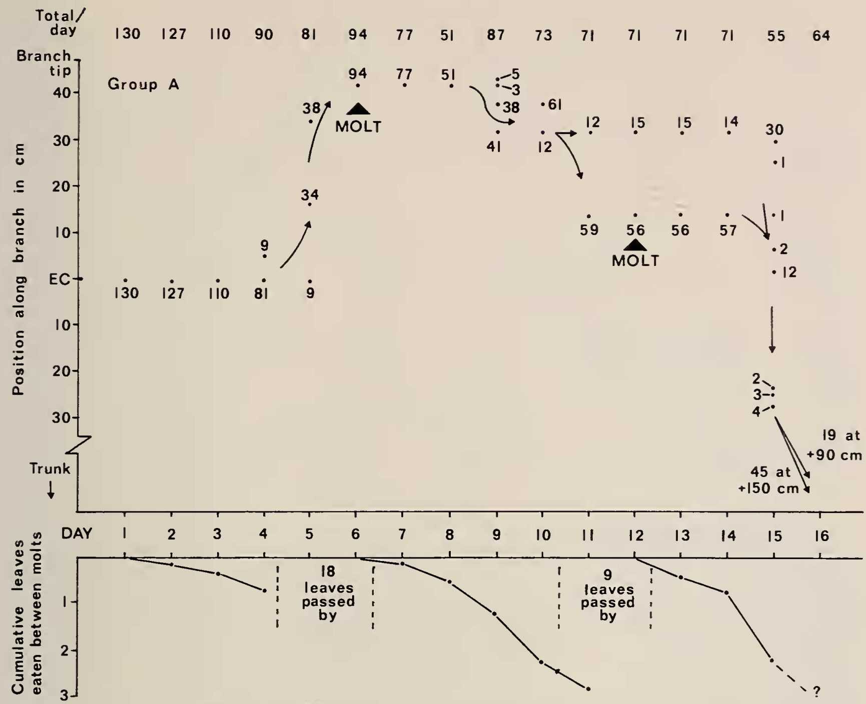

FIG. 1. Foraging behavior of tawny emperor caterpillars, from 24 September through 9 October 1981. EC indicates the position of the egg cluster on the branch. Larval numbers per leaf are shown. Arrows indicate periods of larval movement.

the nearest tenth and then averaged for number of leaves eaten per aggregation per observation.

RESULTS AND DISCUSSION

After hatching, the caterpillars fed on that same leaf and occasionally on adjacent leaves. For example, group A ate 35% of the leaf tissue of two of three adjacent leaves. Group B fed on four adjacent leaves, removing 60% of the leaf material. Five to six days later the larvae moved up to 1.2 m to a new site, passing by numerous leaves and presumably suitable food along the way (Figs. 1 & 2). Reaggregation at the next site took one to two days. Then larvae molted on the underside of a leaf or between adjacent leaves, often tying the edges of the leaf or leaves around them. After molting the larvae fed on those leaves and others on the twig, often leaving only the major leaf veins intact (Fig. 3). Group A fed on seven of eight adjacent leaves, removing 43% of the leaf tissue. Group B ate 34% of four adjacent leaves, subdivided and continued feeding on a few more leaves. Four to six days after the second feeding bout, the larvae moved up to 3.1 m. During

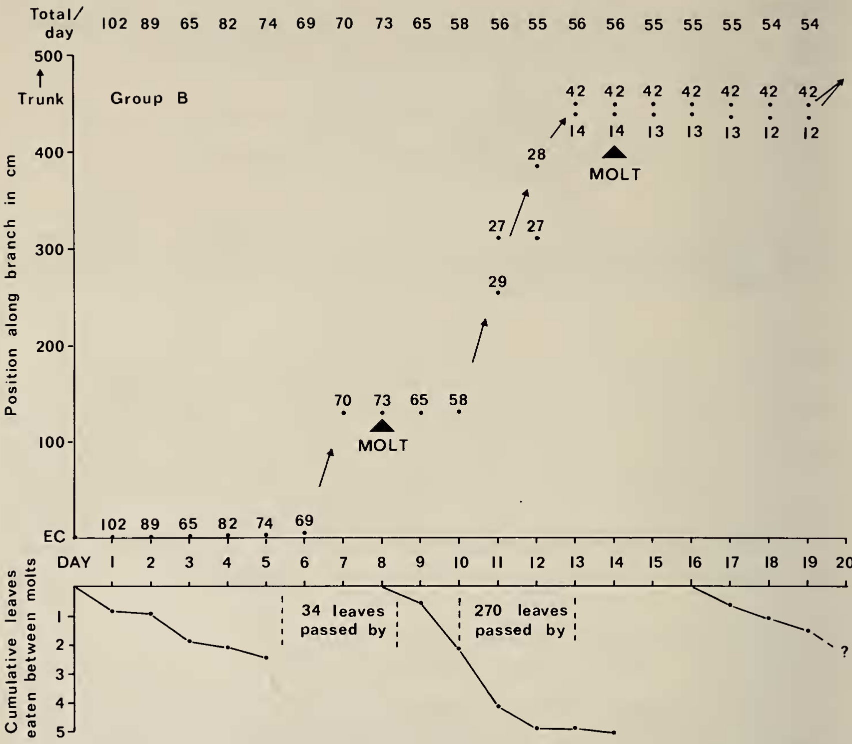

FIG. 2. Foraging behavior of tawny emperor caterpillars, from 24 September through 12 October 1981. EC indicates the position of the egg cluster on the branch. Larval numbers per leaf are shown. Arrows indicate periods of larval movement.

the second migration the larval groups often subdivided, as shown in Figs. 1 & 2. At the third set of sites they molted and then fed, staying there about five to six days.

At the first molting site, 72.3 and 71.5% of the original number of larvae (Figs. 1 & 2, respectively) were present. About half of the original number of larvae were reaggregated at the second molting site (54.6 and 53.9% of those hatching from egg clusters A and B, respectively). Four factors may account for this larval loss. First, the missing larvae may have moved more than 500 cm (length of the major branches) before the second molt; but this seems unlikely. These larvae use silk trails to follow others and remass at new sites. During their migration the caterpillars walk along the branches, with leadership continually changing as the caterpillars pass others momentarily stopped or those backtracking. Consequently, a multi-stranded silk path is deposited which the last caterpillars follow with less rambling than their

FIG. 3. Feeding site of second-instar tawny emperor caterpillars. Approximately 70% of the six distal leaves was eaten. Shaded areas indicate gall tissue that apparently was rejected by the caterpillars.

predecessors. A second factor contributing to larval disappearance may have been caterpillars dropping from the trees in response to disturbance. But as early instars, these caterpillars usually drop on silk threads and then climb the silk back to their feeding site. A third explanation for the decreasing larval numbers may have been that surveying leaves during group molting underestimated larval numbers. But the relatively constant larval numbers during the molting periods suggest that few if any larvae were wandering to and from the groups then (see "Total/day"for second molts, Figs. 1 & 2). Thus, the fourth factor, predation, is probably the major one contributing to larval disappearance. Only 10 dead larvae were found on the leaves, but predators may remove or entirely consume their prey. For instance, pentatomid bugs often carry off caterpillars and feed with their prey suspended from the beak and off the plant (Evans, 1983). Coccinellid beetle larvae may consume all but the head capsule of early instar caterpillars (Stamp, pers. observ.).

The effect of feeding caterpillars aggregating for several days at a site was to concentrate leaf damage. For example, at three feeding sites, all of which occurred at the end of branchlets, 79% of the leaf tissue of six adjacent leaves, 48% of 19 leaves and 73% of 30 leaves were eaten. Consequently, these larval aggregations by way of their leaf damage were easy to locate, and presumably predators and parasitoids find them apparent, also.

These tawny emperor caterpillars exhibited defensive behaviors, such as swinging their heads and attempting to bite with their mandibles when disturbed. The large, laterally-flattened head capsules with numerous protuberances on the edge are used in a shield-like manner when the caterpillars defend themsleves and may be effective against ants and other small predators. These caterpillars are attacked by chalcidoid and ichneumonoid wasps (T. Friedlander, unpubl. data). For instance, 68% of 41 larval sites had parasitized caterpillars, indicated by the presence of parasitic pupae on or around them (Stamp, unpubl. data). (The parasitized caterpillars were left behind when the post-molt individuals moved on.) Also, vespid wasps may remove tawny emperor caterpillars repeatedly, once they locate an aggregation (T. Friedlander, pers. comm.). Thus, it is not clear whether the defenses of these caterpillars would be enhanced by aggregation as the defenses are for other larvae (e.g., thrashing and regurgitating as with aposematic sawfly larvae, Tostowaryk, 1972).

The crypticity, movement away from feeding sites before molting, and tying leaves at molting sites suggest that tawny emperor caterpillars may be especially vulnerable to their enemies when molting. These caterpillars are less defensive then than during non-molting periods. Tawny emperor caterpillars may obtain some advantage from molting together, enclosed by leaves bound with silk, or from overwintering together (at mid-instar), having tied the deciduous leaves securely with multiple silk strands to the tree (Stamp, 1983). Perhaps these advantages outweigh the possible disadvantages that may arise from group feeding (i.e., concentrated leaf damage, which may attract natural enemies).

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